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REGENERATION POSTERIORLY IN ENCHYTRÆUS ALBIDUS[1]

H. R. HUNT

THE primary object of the following experiments was to determine whether *Enchytræus albidus* can regenerate posteriorly, when cut at regions of the body varying from near the posterior end to near the anterior end. Secondly, an attempt was made to compare the rates of regeneration per day posteriorly at the different levels at which the worms were cut in two.

No experiments have been published in which the capacity of this species to regenerate posteriorly has been tested. Nusbaum ('02; '04) studied the histological processes in the regeneration of the Enchytræidæ anteriorly and posteriorly. He found that regeneration anteriorly does not take place as readily as regeneration posteriorly, and that never more than two or three segments regenerate anteriorly.

The animals used in the present experiments were collected in abundance from the coarse gravel of the tidal zone on the seashore at Cold Spring Harbor, Long Island, New York. Six sets of experiments were conducted. Each of the worms was cut into two pieces, the anterior and the posterior pieces being preserved. The average number of segments in this species is not far from sixty. The regions selected for cutting were such as to give fairly comprehensive data as to the regenerative capacity posteriorly at different levels. In the first set of experiments the worms were so cut as to leave only about eight anterior segments; in the second set about sixteen anterior segments; and in the third set about twenty anterior segments. In the fourth set the cut was made near the middle of the worm; in the fifth about sixteen posterior

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[1] Contributions from the Zoological Laboratory of the Museum of Comparative Zoology at Harvard College, No. 260.

segments were removed; and in the sixth eight posterior segments. The worms were anesthetized with chloretone, and the operation was performed under a dissecting microscope. The pieces were placed in small sterilized glass bottles, each containing a strip of filter paper and enough sterilized sea water to keep the animals well moistened. Ten pieces of approximately the same length were kept in a single bottle. Throughout the experiment the bottles, each one stoppered with a cork, were kept in an ice chest to restrict the growth of bacteria. The work was begun early in July, 1913, and was continued until the first of October. At the middle of August it became necessary to carry away from the seashore the material then living. After this, fresh water was used for moistening the worms and cleaning out the bottles. The worms, however, seemed to regenerate as well in the fresh-water as in the salt-water environment. The analysis of the results of the experiments was done in the zoological laboratory of Harvard University.

It was found that the *length* of the regenerated segments, as compared with that of the segments in the adjacent unregenerated part of the worm, was a fairly accurate criterion for determining the number of regenerated segments. To test the accuracy of this criterion, parts of eight worms consisting of the twenty most anterior segments were allowed to regenerate for about eight weeks. Having taken the precaution to determine accurately the number of segments in each of the pieces at the time of the operation, it was easy to determine how many segments had regenerated, for of the total number of segments at the end of the experiment all except the original twenty were, of course, regenerated segments. The result thus obtained was compared in each worm with that obtained by counting in the same worm the number of segments posterior to the point where there was an abrupt change in the length of the segments, that point indicating the region of the cut. Table I gives the data for this comparison. The results show that the method which was used to determine the number of regenerated segments is accurate to within one or two segments, for it will be noted that the results by the two methods never differ by more than two segments, usually by only one. The worm's body is so short that it was found impracticable to secure exactly eight, sixteen, etc., segments in every piece used in the whole series of experiments.

TABLE I

	Number of Segments Regenerated	
Number of the Worm	Total Number Minus 20	As Determined by Segment Length
1	6	7
2	18	18
3	20	22
4	23	24
5	21	22
6	15	14
7	18	17
8	10	12

The results obtained in each of the six sets of experiments have been condensed, for convenience, and are shown in Table II. In the first vertical column of this table the Roman numerals designate the number of the set of experiments. The horizontal lines corresponding to each of these sets give in succession, (1) the number of segments in the pieces used in the experiments, (2) the number of worms operated on, (3) the number that survived long enough to be observed, (4) the per cent of worms that survived and were observed, (5) the period during which the regeneration took place, (6) the number of segments (0 to 24) regenerated by the surviving worms, (7) the average number of segments regenerated in each set of experiments, and (8) the mean rate of regeneration per day of the worms in each set expressed in segments. This mean rate of regeneration was obtained by first computing the rate of regeneration per day (in segments) for each worm in the set, and then averaging all the results. In some worms the number of segments regenerated was observed twice, several weeks elapsing be-

TABLE II

No. of the Set of Experiments	No. of Segments Removed[1]	No. of Worms Operated	No. of Worms Observed	Percentage Surviving	Period of Observation	Number of Individuals Regenerating from 0 to 24 Segments Each																									Average No. of Segments	Rate per Day in Segments
						0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24		
I	52	95	6	6	36 days	..	..	..	1	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	5.0	.146
					57 "	..	..	..	..	..	..	..	1	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	9.0	
II	44	129	31	24	21–29 "	6	1	2	..	2	..	..	1	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2.9	.207
					34–35 "	..	..	..	..	..	2	..	1	2	3	2	1	1	..	1	1	..	..	..	..	..	..	..	..	..	9.4	
					60–81 "	..	..	..	..	..	..	..	1	1	..	..	1	..	..	..	..	3	..	..	1	..	1	2	..	..	15.8	
III	40	30	10	33	44–59 "	..	..	..	..	..	..	2	1	..	..	..	..	1	..	1	..	..	1	1	..	..	..	2	..	1	14.8	.267
IV	30	110	44	40	33–36 "	1	..	..	..	..	1	4	2	7	5	2	1	1	1	1	1	..	..	..	..	..	..	..	..	..	8.8	.238
					41–49 "	..	..	..	..	..	2	..	..	3	3	1	..	1	1	1	..	..	..	..	..	..	..	..	..	..	9.2	
					72–83 "	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	3	..	2	5	1	1	2	5	..	..	18.7	
V	16	164	51	31	26–31 "	5	3	3	..	6	4	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3.2	.129
					40–48 "	..	1	1	..	1	3	2	5	2	1	..	2	..	..	..	..	..	..	..	..	..	..	..	..	..	6.4	
					64–77 "	3	..	..	..	..	..	..	..	1	3	1	1	1	..	..	1	1	..	..	1	..	..	..	..	..	11.8	
VI	8	100	18	18	25–31 "	..	4	1	2	2	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2.8	.084
					62–79 "	..	3	1	..	..	..	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3.7	
Total.		628	160																													

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[1] The average number of segments in the body is about sixty.

tween the two observations, so that the total number of observations recorded in any one set of experiments may be larger than the number of worms observed in the same set.

The results of these experiments are summarized in the graph shown in Fig. 1, where the rates of regeneration per day (expressed in hundredths of the length of one segment) are measured on the axis of ordinates (Y), and the length (in number of segments) of the pieces that produced the regenerated parts, are measured on the axis of abscissæ (X). Since sixty is about the average number of segments in this species, that is the value which has been used in plotting the curve. A mathematical analysis of the rates of regeneration at the different levels shows that the difference in the mean rates of regeneration at any two successive levels is significant. But the temperature of the worms was not carefully controlled, and the periods during which the wounds were healing and the worms preparing to form new segments were included in the computation of the mean rates of regeneration. Therefore, the ratio between the rates of regeneration, as here computed, at any two of the six levels only approximates the ratio which would have been obtained between the rates at these two levels by subjecting all the worms to the same temperature conditions and by using in the computation of the mean rates of regeneration only the periods during which the segments were being formed. The curve *suggests,* however, that the rate of regeneration for the posterior half of the body is proportional, or nearly so, to the number of segments removed. Anterior to the twentieth segment the rate of regeneration decreases. May we not have here a curve depending on two opposing sets of factors; one which tends to increase the rate of regeneration as more segments are removed, the other to decrease the rate? In the latter set of factors the amount of available building material may be the most important element.

The worms seemed to regenerate equally well in a fresh-water or in a salt-water environment. Thirty-one of the one hundred and sixty surviving worms lived for about forty days in a fresh-water environment and regenerated. Twenty-six worms from which the sixteen posterior segments had been removed, and twenty-six others from which the posterior half had been removed, regenerated almost contemporaneously for about thirty days in the same ice chest, and in a salt-water environment. Later in the season in a different ice chest eighteen worms from which the sixteen posterior segments had been removed, and thirteen from which the posterior halves had been removed, regenerated contemporaneously for about forty days in a fresh-water environment. When the sixteen posterior segments were removed the rate of regeneration in the salt-water environment was 0.02 segments per day *less* than in the fresh-water environment, while when the posterior halves were removed the rate of regeneration in the salt-water was 0.07 segments per day *greater* than in

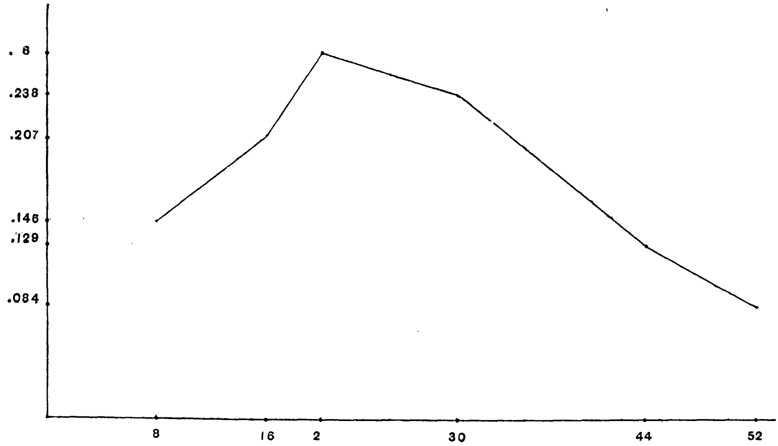
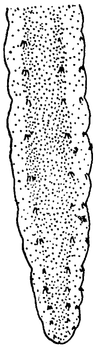


FIG. 1. Curve showing the daily rate of regeneration by pieces of six different lengths. The unit selected to measure the mean rate of regeneration at each of the six levels was 1/100 of a segment, while that used to measure the lengths of the pieces which produced the regenerated segments was *one* segment. In plotting the curve the length selected to represent 1/100 of a regenerated segment (on axis Y) was the same as that chosen to represent one segment (axis of X) of the pieces producing the regenerated parts.

the fresh-water surroundings. These facts show that the worms regenerate in both fresh and salt water. This is not surprising, since individuals of this species are normally found both on the seashore, where they live in a salt-water environment, and also in earth moistened with fresh water. Furthermore, with the exception of the salinity of the water used to moisten the worms, the worms which regenerated in the fresh-water surroundings were probably subjected to about the same conditions as those which regenerated in the salt-water. Therefore, the salinity of the water in the environment does not seem to affect the rate of regeneration. The data used in plotting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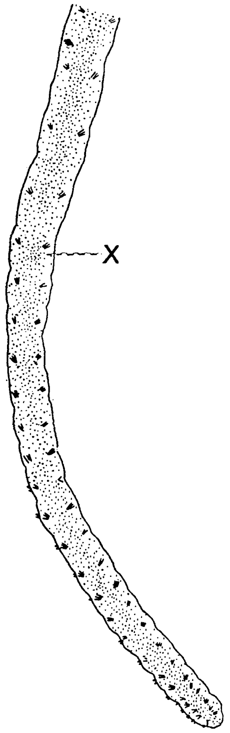

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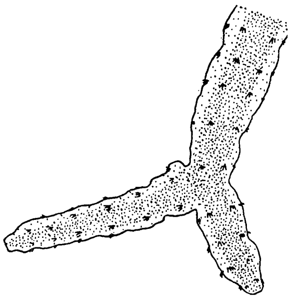
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FIG. 2. Camera lucida drawing of the posterior end of a normal worm. Magnified 17 diameters.

FIG. 3. Camera lucida drawing showing the regenerated posterior end of a worm. The region posterior to *X* is regenerated. Magnified 17 diameters.

FIG. 4. Sketch of a regenerated double tail. Magnified about 17 diameters.

the curve shown in Fig. 1 were secured from worms which regenerated in the fresh-water, as well as from those which regenerated in the salt-water, environment. The above observations make it seem probable, therefore, that the form of the curve does not differ fundamentally from the form which it would have had if all the worms had regenerated in salt-water surroundings.

In. Fig. 2 is shown the normal appearance of the ventral aspect of the posterior end of a worm in which there has been no regeneration. It will be noticed that the length of the segments gradually decreases toward the posterior end; but in Fig. 3, which is a camera lucida drawing of the posterior portion of one of the regenerated worms, the length of the segments decreases abruptly at the point *X*, showing that to be the point at which the tail was removed.

Three worms from which eight posterior segments were removed regenerated double tails. Morgan ('97) and Michel ('98) observed the same phenomena in *Allolobophora fœtida*. One of these worms is shown in Fig. 4.

Some attempts were made to determine the rate of regeneration anteriorly at different levels on the worm's body. At present all that can be said is that regeneration posteriorly takes place much more frequently and rapidly than anteriorly.

The conclusions that follow from these experiments are:

1. *Enchytræus albidus* regenerates posteriorly when cut off at any level between eight segments from the posterior end of the body and eight segments from the anterior end. It will be noticed that although the mortality in pieces containing only the eight most anterior segments was about 94 per cent., yet those that did survive regenerated from three to eleven (on the average seven) segments. In other words, a piece from the extreme anterior end, containing only one eighth the number of segments in the whole worm, can regenerate nearly as many segments, on the average, as it had at the beginning of the experiment. Morgan ('97) found that in *Allolobophora*

fœtida anterior pieces of less than thirteen segments rarely, if ever, regenerate posteriorly. In *Enchytræus* the anterior limit of the capacity to regenerate posteriorly was not found.

2. The rate of regeneration seems to increase from the posterior end of the worm up to its middle almost in direct proportion to the number of segments removed. Anterior to about the twentieth segment the rate decreases.

3. Regeneration can take place either in a fresh-water or in a salt-water environment. Also, the salinity of the water seems to have little or no effect upon the rate of regeneration.

4. Double tails can be regenerated when the eight most posterior segments are removed.

5. Regeneration posteriorly takes place more readily than it does anteriorly.

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